THE CRETACEOUS AMMONITE GENUS *LEYMERIELLA*, WITH A SYSTEMATIC ACCOUNT OF ITS BRITISH OCCURRENCES

by RAYMOND CASEY

ABSTRACT. Ammonites of the genus *Leymeriella* Jacob characterize the Northern Hemisphere and are found in neritic deposits of Lower Albian age extending from the Urals to east Greenland. Known occurrences are restricted to the Zone of *Leymeriella tardefurcata*. Investigation of anomalous records of *Leymeriella* in the overlying Zone of *Douvilleiceras mammillatum* discloses that the classic 'Mammillatum' bed of the Ardennes and Meuse Departments of France, which furnished d'Orbigny with much type material, is a condensed deposit in which elements of both Tardefurcata and Mammillatum age are combined. Account is taken of 18 species and 3 varieties of *Leymeriella* (including the subgenus *Epileymeriella* Breistroffer), of which 4 species and 1 variety are new, and 4 species of *Proleymeriella* Breistroffer, 1 new. Systematic treatment is given 7 species and 3 varieties of *Leymeriella* of British provenance.

Mode of coiling, ontogenetic development of the septal sutures, and certain sculptural features indicate that the affinities of *Leymeriella* lie with the Lyelliceratidae (Acanthocerataceae) rather than with the Hoplitidae (Hoplitaceae) to which it has been generally attached. It is believed that *Leymeriella* provides the key to the origin of the great ammonite superfamily Acanthocerataceae. An eruptive phase of evolution at the beginning of the Albian is postulated in which the Lyelliceratidae (including Leymeriellinae), Brancoceratidae, and Mojsisovicsiidae are conceived as simultaneous and rapidly differentiating offshoots of the Desmoceratid *Callizoniceras*. Support for this hypothesis is given by '*Hoplites*' *haidaquensis* Whiteaves, from the Albian of the Queen Charlotte Islands, a member of the Lyelliceratid-Brancoceratid complex for which the nominal genus *Pseudoleymeriella* is proposed. It is suggested that the Acanthocerataceae and the Hoplitaceae may represent synchronous radiations from the Lytocerataceae and Phylloceratacea respectively.

Leymeriellinae and Hoplitinae may have been mutually exclusive, the one shunning areas favourable to the other. The apparent extinction of *Leymeriella* coincided with the appearance in Europe of new, virile Hoplitid stocks in the Mammillatum Zone.

INTRODUCTION

Leymeriella is a closely integrated group of Lower Cretaceous ammonites whose evolution, geographic dispersal, and extinction have features of unusual interest to the palaeontologist. Confined to the base of the Albian, yet with a wide distribution throughout Europe, it forms an excellent horizon-maker and its two principal species, *L. tardefurcata* (d'Orb.) and *L. regularis* (Brug.), have figured prominently in literature relating to Albian stratigraphy and zonal classification. Since the time of its description by Jacob (1907, 1908) the genus has been studied principally by Spath (1925), Seitz (1930), Brinkmann (1937), and Breistroffer (1947). To Brinkmann we owe a convincing demonstration of the origin of *Leymeriella* in the Desmoceratid *Callizoniceras*.

The present paper is an extract from a thesis on the Ammonoidea of the Lower Greensand formation of southern England prepared in the Geology Department of the University of Reading during a period of leave kindly granted the author by the Department of Scientific and Industrial Research. The nucleus of this extract is a systematic account of British occurrences of *Leymeriella*. Data obtained in the course of this research have led to conclusions of wider interest concerning the systematic position, distribution and ecology of the genus such as to justify advance publication.

[Palaeontology, Vol. 1, Part 1, 1957, pp. 28–59, pls. 7–10]

The author acknowledges with gratitude a grant from the Royal Society towards the expenses of his research on the Lower Greensand Ammonoidea. Acknowledgements are also made to the Director of the Geological Survey of Great Britain and to the late Dr. L. F. Spath of the British Museum (Natural History) for access to the collections in those institutions. Similar facilities were provided in Paris by Dr. J. Roger (Muséum d'Histoire Naturelle), Professor P. Pruvost (Sorbonne), and Mme D. Létia (École Nationale Supérieure des Mines). A special word of thanks is due to Mr. C. W. Wright, who has granted free use of the superb collection of Cretaceous ammonites made by him and his brother, Mr. E. V. Wright. Dr. J. A. Jeletzky of the Geological Survey of Canada kindly supplied casts of *Hoplites haidaquensis*.

Specimens collected in the course of the author's field work have been deposited in the Geological Survey Museum. The paper is published by permission of the Director of the Geological Survey of Great Britain.

MORPHOLOGY AND SYSTEMATIC POSITION OF *LEYMERIELLA*

As originally described by Jacob (1907, p. 368) *Leymeriella* was merely a subdivision of a broad genus *Hoplites* Neumayr, and the only taxonomic criteria mentioned were the single ribbing and simple suture-line. A fuller description was later published (Jacob 1908, p. 47) as follows:

> La coquille a des côtes généralement simples, peu flexueuses, interrompues par un sillon sur la région siphonale. La cloison, peu divisée, comporte un premier lobe latéral profond, symétrique; elle est surtout caractérisée par l'allure particulière de deux selles auxiliaires, qui forment un ensemble perpendiculaire à la suture ou même gagnant vers la bouche du côté de l'ombilic.

No type species was named and of the two species originally included in the genus by Jacob, namely *A. tardefurcatus* (Leymerie MS.) d'Orbigny and *Ammonites regularis* Bruguière, Spath (1925, p. 75) designated *A. tardefurcatus* as the type. Mme Basse (1952, p. 656) and Wright (1957, p. 392), however, cite *A. regularis* as the type, the latter author signifying that this type fixation was by original designation.

Seitz (1930) divided *Leymeriella* into two groups: (1) discoidal forms without tubercles on the flanks, such as *L. tardefurcata* (d'Orb.), *L. rencurelensis* (Jacob), *L. romani* (Jacob), *L. revili* (Jacob), and *L. hitzeli* (Jacob) and (2) more robust forms with both ventral and umbilico-lateral tubercles, typified by *L. regularis* (Brug.) and *L. pseudoregularis* Seitz. These two groups correspond roughly to two lineages of *Leymeriella* conceived by Brinkmann (1937) as having diverged from a common ancestry in the group of *L. schrammeni* at the base of the Tardefurcata Zone of the Lower Albian. The existence at the top of the Tardefurcata Zone of a host of species showing every gradation between the *tardefurcata* and *regularis* types suggests that Seitz and Brinkmann oversimplified the taxonomic and phylogenetic relationships within this 'genus'.

A more acceptable classification of *Leymeriella* and its allies was made by Breistroffer (1947). This author separated from *Leymeriella* s.s. the two subgenera *Proleymeriella* (for the group of '*Parahoplites*' *schrammeni* Jacob) and *Epileymeriella* (for the group of '*Parahoplites*' *hitzeli* Jacob). The former is an early development, untuberculated, and with ribs that sometimes branch on the flanks and which form chevrons on the venter. Its degree of morphological differentiation from *Leymeriella* is here considered sufficient

to warrant full generic status. *Epileymeriella*, also without tubercles, is further characterized by the costae being unusually deeply and widely split, each branch tending to split again, so that double bifurcation is frequently produced.

Separation of *Leymeriella* as a distinct subfamily of the Hoplitidae was made independently by Breistroffer (1951, p. 266) and Wright (1952, p. 220), Breistroffer having priority. Later (1955, p. 571) Wright promoted it to family status within the Hoplitaceae on the grounds that its origin was too distinct to be included in the restricted Hoplitidae.

An important outcome of the present research is the recognition that *Leymeriella*, long classed with the Hoplitids, is a primitive member of the Lyelliceratidae. This family was created by Spath originally for the genera *Lyelliceras* Spath, *Neophlycticeras* Spath, and *Stoliczkaia* Neumayr, to which were subsequently added *Prolyelliceras* Spath, *Tegoceras* Hyatt (= *Rauliniceras* H. Douvillé), and *Budaiceras* Böse. It now comprises a host of Albian and basal Cenomanian genera, mostly unrepresented in Britain, and has been divided by Breistroffer (1953) into the two subfamilies Lyelliceratinae and Stoliczkainae. The last, being exclusively of Upper Albian and basal Cenomanian age, need not be considered further.

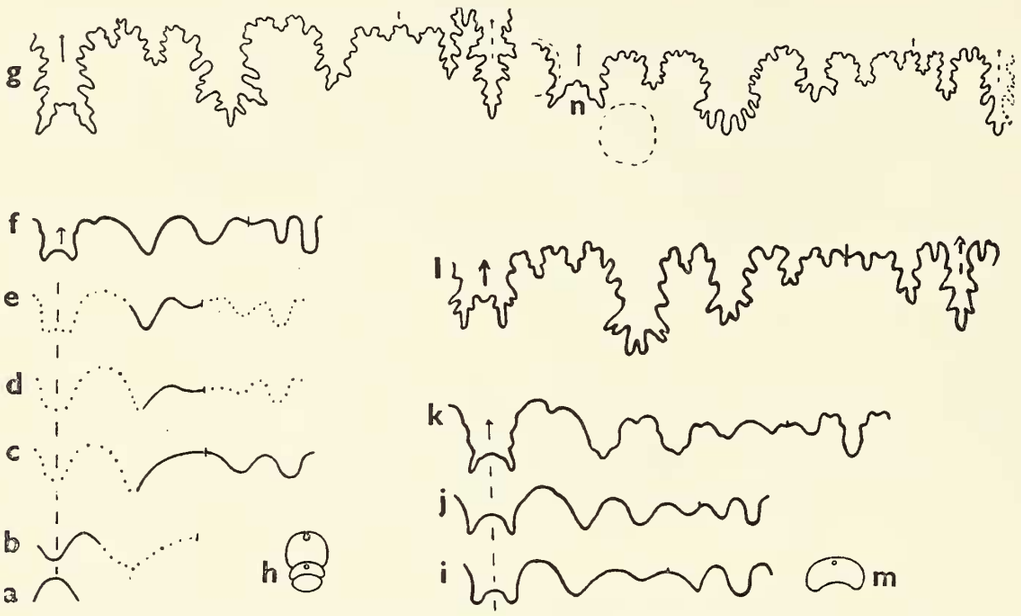
The family exhibits a diversity of morphological types and, as pointed out by Spath (1931, p. 313), while the siphonal row of tubercles is a distinctive feature of the Lyelliceratidae, yet some forms have the ventral aspect of *Hoplites* (i.e. a sulcate periphery) and others that of *Sonneratia* (i.e. an arched venter with strong costation continuous across the periphery).

Leymeriella as here interpreted encompasses a group of primitive Lyelliceratids that are characterized by loose coiling, shallow umbilicus, and venters of Hoplitid aspect. The suture-line is rather simple, with bifid saddles, a deep, parallel-sided ventral lobe and trifid lateral lobes, the auxiliaries showing little or no umbilical retraction. The whorls are generally compressed and of a basic subrectangular shape that may be modified to subhexagonal by the acquisition of ventral and umbilico-lateral tubercles. The ribs are uniform, straight or sigmoidal, and are generally flattened and grooved on the outer half of the whorl-side as though bifurcating. Near the umbilicus the ribs may be pinched up into a flare or may bear a distinct spinose tubercle; their ventral terminations usually form clavi bordering a median ventral sulcation, each clavus placed in line with its fellow on the opposite side of the venter. The umbilical wall is seldom steeply sloped and has no definite rim. Widening of the umbilicus, loss of tuberculation, and crowding of the ribbing are features of maturity. 'Gerontic' specimens may exhibit constrictions and ventral ribs that unite in the form of chevrons. The body-chamber occupies about half a whorl and terminates in a plain mouth-border.

Grounds for transferring *Leymeriella* to the Lyelliceratidae may be stated as follows:

Coiling. Ignoring the immediate post-embryonic whorls, in which, as in most ammonites, there is a rapid change in geometric relations, the shell of *Leymeriella* forms a slowly unwinding spiral. The degree of overlap of the whorls is never very profound and decreases with age until, at say 70–80 mm. diameter, the whorls are merely in contact, only the ventral tubercles leaving an impression on the dorsum of the last whorl. This condition of coiling is paralleled in *Lyelliceras* and *Prolyelliceras*. In the Hoplitidae, which grow to a much larger size, relatively tight coiling and a well-impressed dorsum are maintained through life.

Suture-line. The ontogenetic development of the suture-line of *Leymeriella* has been worked out by dissection of immature specimens of *L. consueta* sp. nov. of the Regularis Subzone and is illustrated in text-fig. 1. The first suture-line, *a*, may be assumed to be of the angustisellate type common to the embryonal stage of all post-Triassic ammonites, though only the high external saddle could be made out. It will be observed that the second and third sutures, *b* and *c*, possess a shallow ventral lobe and two broad saddles

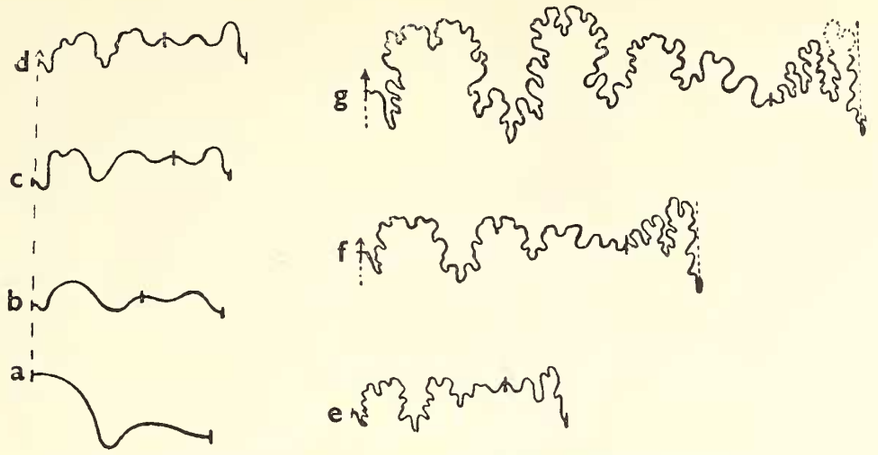


TEXT-FIG. 1. Suture-lines and early whorls of Lyelliceratidae. *a–h*, *Leymeriella* (*Leymeriella*) *consueta* sp. nov. *a*, *b*, *c*, *d*, *e* = 1st, 2nd, 3rd, 9th, and 12th sutures; *f* = suture-line at 1·75 mm. diameter; *h* = protoconch and first two whorls. W.W. 8410, Regularis Subzone (Band I), Arnold's Pit, Leighton Buzzard, Beds.; *g* = suture-line at *c.* 45 mm. diameter, enlarged ×2·5. Locality and horizon as before. Author's Coll., G.S.M. Zm 2024.

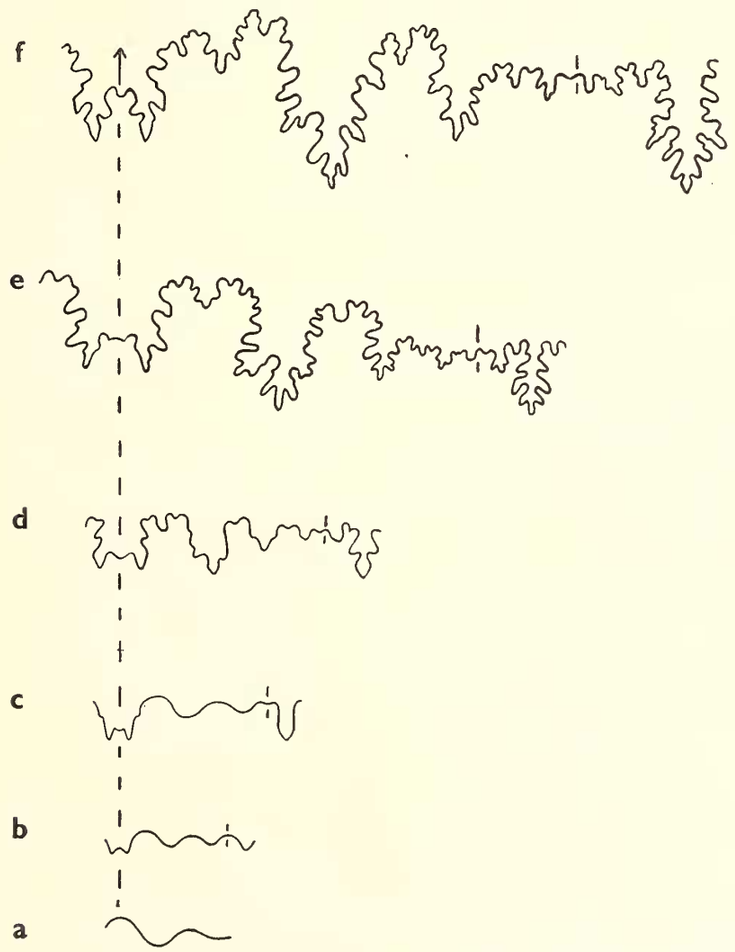
i–m, *Lyelliceras lyelli* (d'Orbigny). *i*, *j*, *k* = suture-lines at 1·5, 2, and 4 mm. diameter; *m* = whorl-section at 1·5 mm. diameter. F. G. H. Price Coll., G.S.M. FOR. 58, Middle Albian (Dentatus Zone), Gaty, France; *l* = suture-line at 20 mm. diameter. Locality, horizon, and collector as before. G.S.M. FOR. 57.

n, *Tegoceras gladiator* (Bayle). Complete suture-line at 40 mm. diameter. Author's Coll., G.S.M. Zm 2023, Mammillatum Zone, Ford Place, Wrotham, Kent.

that are separated by a deep, V-shaped lateral lobe; internally a well-developed umbilical lobe is already present adjacent to the antisiphonal lobe. In subsequent growth stages, *d* and *e*, the second lateral lobe originates as an embayment of the broad lateral saddle and is later pushed outwards up the flank as the second lateral saddle ripples out from the umbilical seam. By the second whorl, *f*, when the ammonite is still less than 2 mm. diameter, the elements of the adult suture-line have been laid down and there is no further development beyond minute elaboration of this basic pattern. Shortening of the internal suture-line, accompanied by some degree of atrophy of the umbilical lobe, is a mechanical adjustment to the rapid change in whorl-shape from cadicone to subrectangular, strikingly exhibited in the first two volutions (text-fig. 1*h*). Thus the sutural development of *Leymeriella* takes place mainly on the external side, the internal portion retaining throughout ontogeny only the elements present in the primitive suture-line. This contrasts sharply with the growth of sutural characters in the Hoplitidae (text-fig. 2), but is



TEXT-FIG. 2. Suture-line development of a Hoplitid ammonite. *a*, *b* = 1st and 2nd sutures; *c*, *d*, *e*, *f*, *g* = suture-lines at 2·5, 4, 5, 8, and 17 mm. diameter; *f* and *g* based on specimens of '*Hoplites auritus*' (Price *non* J. Sowerby) from the Middle Gault of Dunton Green, Kent. After Spath, Monograph of Gault Ammonites, text-fig. 1.



TEXT-FIG. 3. Suture-line development of *Deshayesites deshayesi* (Leymerie MS.) d'Orbigny sp. *a*, *b* = 1st and 2nd sutures, from a topotype in the Sorbonne Coll., Lower Aptian (Deshayesi Zone), Bailly-aux-Forges (Haute-Marne); *c*, *d*, *e* = suture-lines at 2, 8, and 16 mm. diameter; same horizon and collection, St. Dizier (Haute-Marne); *f* = suture-line at 34 mm. diameter; horizon, locality, and collection as for *a*, *b*.

normal for the Lyelliceratidae, as I have ascertained by study of juvenile specimens of *Lyelliceras*. It is only necessary to compare the external suture-lines of *Leymeriella* with those of *Lyelliceras* as figured by d'Orbigny (1841, pl. 74, fig. 6) and Pictet and Campiche (1859, pl. 24, figs. 6*c*, 9) to appreciate the essential similarities, especially in the almost radial course of the septal edge across the flank. These similarities are enhanced when comparison is made with the complete suture-line of *Lyelliceras* or *Tegoceras* (text-fig. 1, *i–n*). In the retardation of development of the internal portion of the suture-line the Lyelliceratidae recall the Deshayesitidae of the Aptian (text-fig. 3) rather than the Hoplitidae. In the last family the septal edge has a strong umbilical retraction and the suture-line is folded into numerous lobes and saddles on both sides of the umbilical seam.

Sculpture. No Hoplitid ammonite possesses the single, uniform ribbing of *Leymeriella*; such ribbing is altogether typical of the early Lyelliceratidae, *Lyelliceras*, *Prolyelliceras*, and *Tegoceras*. Compare, for instance, the lateral aspect of *Leymeriella rudis* sp. nov. (Pl. 8, fig. 6) and *Tegoceras gladiator* (Bayle) (Pl. 7, fig. 8) or of the species of *Leymeriella* and *Prolyelliceras* illustrated in Pl. 7. Umbilico-lateral tuberculation arises in *Leymeriella* from the pinching up of the ribs near the umbilicus; this structure is strictly homologous with the lateral bulge of the ribs in *T. gladiator* and is quite different from the bullate tubercles found in the Hoplitidae. The paired ventral clavi of *Leymeriella* offer a strong similarity to those of the Hoplitidae. Here again, this genus merely carries to extremes a tendency manifest in *T. gladiator*, the zigzag ventral ribbing of which simulates that of its Hoplitid contemporary *Otohoplites*.

EXPLANATION OF PLATE 7

Figs. 1, 1*a–c*. *Pseudoleymeriella haidaquensis* (Whiteaves), Lower Albian (Haida Formation), Skidegate Inlet, Queen Charlotte Islands. Plaster cast of holotype (1, 1*a*) with suture-line, enlarged ×4 (1*b*) and whorl-section (1*c*). Geol. Surv. Canada 5991.

Figs. 2, 2*a*. *Proleymeriella schrammeni* (Jacob), Tardefurcata Zone (Schrammeni Subzone), Algermissen, Hanover. Topotype. B.M. C. 14398; A. Schrammen Coll.

Figs. 3, 3*a*. *Proleymeriella phoenix* sp. nov. Locality and horizon as for Fig. 2. B.M. C. 14397; A. Schrammen Coll.

Figs. 4, 4*a*. *Callizoniceras* (*Wollemanniceras*) *keilhacki* (Wollemann), Upper Aptian, Nodosocostatum Zone (Jacobi Subzone), Schwiecheldt, Hanover. W.W. G 831.

Fig. 5. *Callizoniceras* (*Wollemanniceras*) *keilhacki* (Wollemann), Upper Aptian, Nodosocostatum Zone (Jacobi Subzone), Algermissen, Hanover. Copy of Wollemann 1904, pl. 5, fig. 5.

Fig. 6. *Prolyelliceras* sp., transitional to *Brancoceras*, condensed Lower–Middle Albian, Pielle (Alpes Maritimes). W.W. F 1, ×2.

Figs. 7, 7*a*. *Proleymeriella schrammeni* (Jacob), Tardefurcata Zone (Schrammeni Subzone), Schwiecheldt, Hanover. Side view and whorl-section of nucleus. W.W. G 821, ×2.

Figs. 8, 8*a*. *Tegoceras gladiator* (Bayle). Locality and horizon as for Fig. 6. Side view and whorl-section. W.W. F 2.

Fig. 9. *Leymeriella* (*Leymeriella*) *tardefurcata* (Leymerie MS.) d'Orbigny sp., condensed Lower–Middle Albian of Près de Rencurel (Isère). Copy of Jacob 1908, pl. vii, fig. 12*a*.

Fig. 10. *Leymeriella* (*Leymeriella*) *rudis* sp. nov., Lower Greensand, Tardefurcata Zone (Regularis Subzone), Band I, Arnold's Pit, Leighton Buzzard, Beds. Plasticine impression of a natural mould. W.W. 20547.

Fig. 11. *Proleymeriella* sp. aff. *gevreyi* (Jacob), Gault, Middle Albian, Dentatus Zone, Dienville (Aube). G.S.M. FOR 65; F. G. H. Price Coll.

Fig. 12, 12*a*. *Eubrancoceras* sp., Gault, Middle Albian, Dentatus Zone (Dentatus-spathi Subzone), Colley Lane Pit, Reigate, Surrey. R. A. Beaney Coll.

1

1*a*

1*b* ×4

2*a*

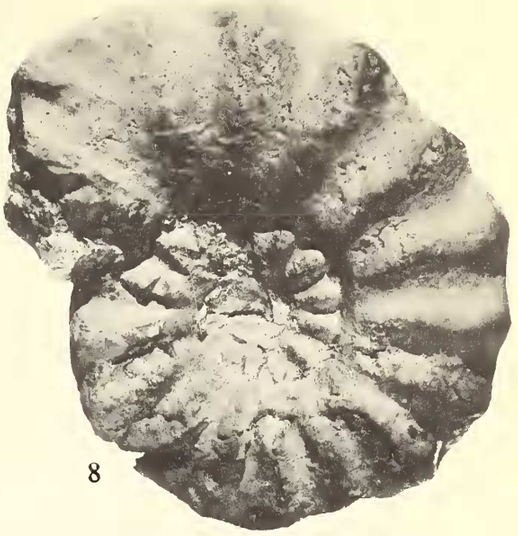
2

3*a*

3

4

4*a*



8

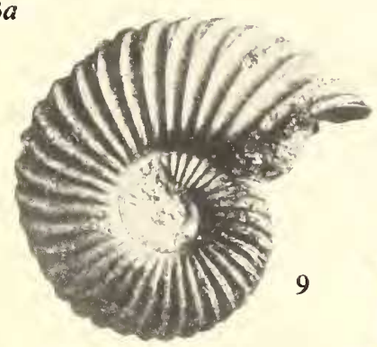
8*a*

7*a*

5

×2

7



9

1*c*

×2

6

10

11

12

12*a*

CASEY, Early Acanthocerataceae

Turning now to the wider field of Albian Acanthocerataceae, we may note other morphological parallels that give support for the inclusion of the Leymeriellinae in this superfamily. Reference may first be made to the likeness of *Proleymeriella* and the Brancoceratidae, a family that is intimately connected with the Lyelliceratidae and the Mojsisovicsiidae. On Pl. 7, figs. 3, 3*a* is illustrated an inflated development of *Proleymeriella*, *P. phoenix* sp. nov., that differs from *P. lemoinei* (Jacob) in its coarser, less flexuous, and sharper ribbing, the ribs being rarely divided and strongly elevated on the venter. But for the high relief and chevron-like extension of the ventral costation this species might have passed for a *Eubrancoceras*; and it is interesting to observe that a species of *Eubrancoceras*, similar to that illustrated on Pl. 7, figs. 12, 12*a*, has been figured from Peru by Steinmann (1929, p. 123, fig. 134) as *Parahoplites* aff. *schrammeni* Jacob. On the same plate I am figuring the early whorls of *P. schrammeni* and of a *Brancoceras-Prolyelliceras* hybrid for comparison with those of *Lyelliceras ulrichi* Knetchel, illustrated by Benavides-Cáceres (1956, pl. 51, figs. 6–7). The fact that they are all strikingly similar to *Callizoniceras keilhacki* (Wollemann) (Pl. 7, fig. 5), the ancestor of *P. schrammeni*, and are easily separable from juvenile Hoplitidae is at once apparent.

Another important link between the Brancoceratid-Lyelliceratid complex and the Leymeriellinae is provided by *Pseudoleymeriella* gen. nov., at present known only by its type species, *Hoplites haidaquensis* Whiteaves (holotype the original of Whiteaves 1893, p. 444, pl. 7, figs. 2, 2*a–b*) from the Lower Albian (Haida Formation) of the Queen Charlotte Islands, and refigured in Pl. 7, figs. 1, 1*a–c*. This differs from all species of *Leymeriella* in its subcircular whorl-section, in the absence of flattening or grooving of the costae, and in not having the terminations of the ribs on each side of the ventral sulcus elevated into forwardly directed clavi. The suture-line is rather simple and combines the deep, narrow ventral lobe of *Leymeriella* with a broad, open first lateral lobe. Breistroffer (1947, p. 70) has commented on the resemblance of the ornament of *Leymeriella crassa* Spath to that of *Mojsisovicsia spinulosa* (Spath). Concerning links with the Mojsisovicsiidae, it may further be noted that the flattening of the costae on the outer part of the flank, one of the most characteristic features of *Leymeriella*, is reproduced in *Mojsisovicsia*, *Oxytropidoceras*, and other primitive members of that family, as well as in *Brancoceras*. *Mojsisovicsia delaruei* (d'Orbigny), of the Middle Albian, at 10 mm. diameter has the same style of costation as immature *Leymeriella tardefurcata*. Grooving of these flattened costae is not a feature of the Mojsisovicsiidae or the Brancoceratidae, it is true. Observe, therefore, the reappearance of grooved and flattened ribs in *Neokentroceras*, an Upper Albian derivative of the Brancoceratidae (see Spath 1921, p. 141, text-fig. D 1, *N. curvicornu*). Remove the keel of *Neokentroceras speciosum* Haas (1942, pl. 8, fig. 14) and we have a life-size morphic equivalent of the adolescent *Leymeriella consueta* var. *magna*, complete with subhexagonal whorl-section, horn-like outer tubercles, and coarse, widely-spaced ribs. It will be unnecessary to labour the point further: the specimens speak for themselves.

It is now suggested that three subfamilies should be recognized in the Lyelliceratidae: (1) Leymeriellinae Breistroffer, exclusively of Lower Albian age, (2) Lyelliceratinae, ranging from Lower to Middle Albian, and (3) Stoliczkainae Breistroffer, of Upper Albian and basal Cenomanian age.

LEYMERIELLA AND THE ORIGIN OF THE ACANTHOCERATACEAE

The case for assimilating the Leymeriellinae to the Lyelliceratidae has been presented above; here it is pertinent to observe that the Lyelliceratidae, appearing in the Lower Albian, are the direct forerunners of the Cenomanian Acanthoceratidae and that they are acknowledged to constitute the main stem from which the superfamily Acanthocerataceae developed. The origin of the Lyelliceratidae themselves is more obscure. Reviewing this family in his Monograph of the Gault Ammonoidea, Spath (1931, p. 314) emphasized the probability of a common origin of the Lyelliceratidae, Mojsisovicsiidae, and the Brancoceratidae, *Brancoceras* being considered closest to the ancestral stock. This ancestral stock was thought to belong most likely to the Parahoplitidae, a view expressed by Spath on a previous occasion (Spath 1922, pp. 108–9) and, before him, by Jacob (1907, p. 361). In the concluding chapters of his Monograph, however, the idea of descent from the Parahoplitidae was abandoned, the discovery of Brancoceratidae with *Silesitoides*-like inner whorls suggesting a more direct liaison with the Desmoceratacea (Spath 1942, p. 710). New collections from the Albian of many parts of the world, but especially from south-east France (e.g. a collection from the Peille (Alpes Maritimes) neighbourhood, made available to me through the good offices of Mr. C. W. Wright), have brought to light so many transitional types between the Lyelliceratidae, Mojsisovicsiidae and the Brancoceratidae, as to leave no room for doubt that these three families are parts of a single genetic complex. For the source of this complex we must examine the clues offered by *Leymeriella*.

Leymeriella is one of the few trachyostracous genera for which there is convincing evidence of ancestry in the Desmoceratacea, the feebly ornamented, long-lived stock which is the theoretical evolutionary reservoir of so many Cretaceous ammonites. Thanks to the work of Brinkmann (1937), referred to above, *Leymeriella* may be traced back to the Desmoceratid *Callizoniceras*. Bed by bed collecting from the uniform suc-

---

EXPLANATION OF PLATE 8

Figs. 1–3. *Leymeriella* (*Leymeriella*) *tardefurcata* (Leymerie MS.) d'Orbigny sp., condensed Regularis-Mammillatum bed of the Ardennes and Meuse Departments of France. 1, 3, 3*a*, two examples leading to var. *intermedia* Spath, from Novion, near Machéroménil (Ardennes) (Muséum d'Histoire Naturelle, Paris; d'Orbigny Coll.). 2, 2*a*, a septate nucleus from Varennes (Meuse) (École des Mines, Paris; Raulin Coll.).

Figs. 4, 4*a*. *Leymeriella* (*Leymeriella*) aff. *consueta* sp. nov., transitional to *L.* (*L.*) *renascens* Seitz, condensed Regularis-Mammillatum bed, Novion, near Machéroménil (Ardennes) (Muséum d'Histoire Naturelle, Paris; d'Orbigny Coll.).

Figs. 5, 5*a–b*. *Leymeriella* (*Leymeriella*) *regularis* (Bruguière) d'Orbigny. Same horizon, Sauces, near Machéroménil (Ardennes). Neotype. Side view (5), ventral view (5*a*), and restored whorl-section (5*c*) (École des Mines, Paris; Raulin Coll.).

Figs. 6, 6*a–b*. *Leymeriella* (*Leymeriella*) *rudis* sp. nov. Side view (6), and front view (6*a*) of holotype, with whorl-section (6*b*) of another specimen. Locality and horizon as for Fig. 4 (Muséum d'Histoire Naturelle, Paris; d'Orbigny Coll.).

Fig. 7. *Leymeriella* (*Leymeriella*) *consueta* var. *magna* nov., nucleus. Locality, horizon, and collection as for Fig. 4.

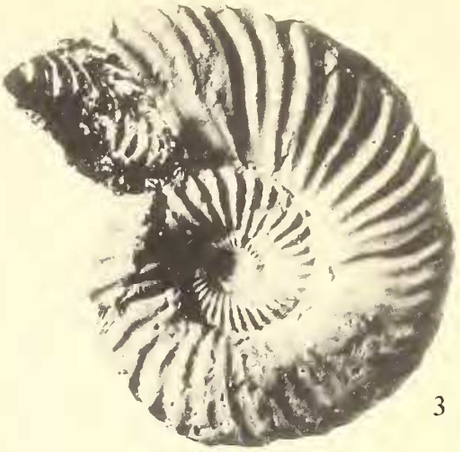
Figs. 8, 8*a*. *Ammonites tardefurcatus* (Leymerie MS.) d'Orbigny, from the Albian of the Aube. Copy of d'Orbigny 1841, pl. 71, figs. 4, 5, slightly reduced.

Figs. 9, 9*a–b*. *Ammonites regularis* (Bruguière) d'Orbigny, from the Albian of the Machéroménil district. Copy of d'Orbigny 1841, pl. 71, figs. 1, 2, 3, slightly reduced.

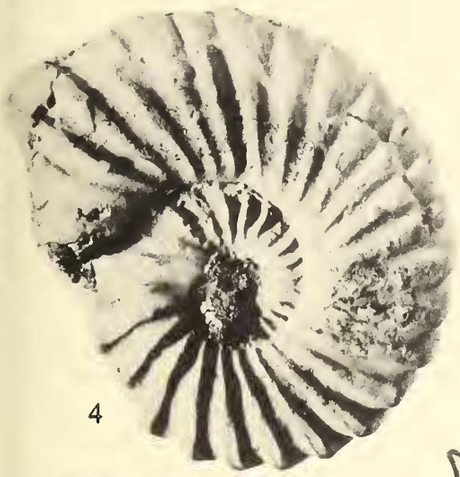
1

2

2*a*



3



4

4*a*

5

5*a*

3*a*

5*b*

6*a*

7

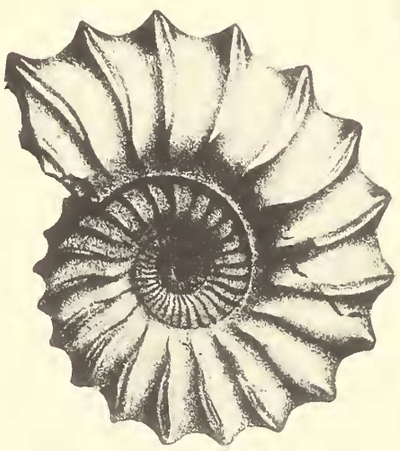
6

6*b*

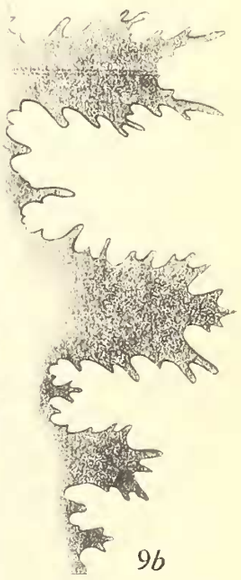
8*a*

8

9*a*



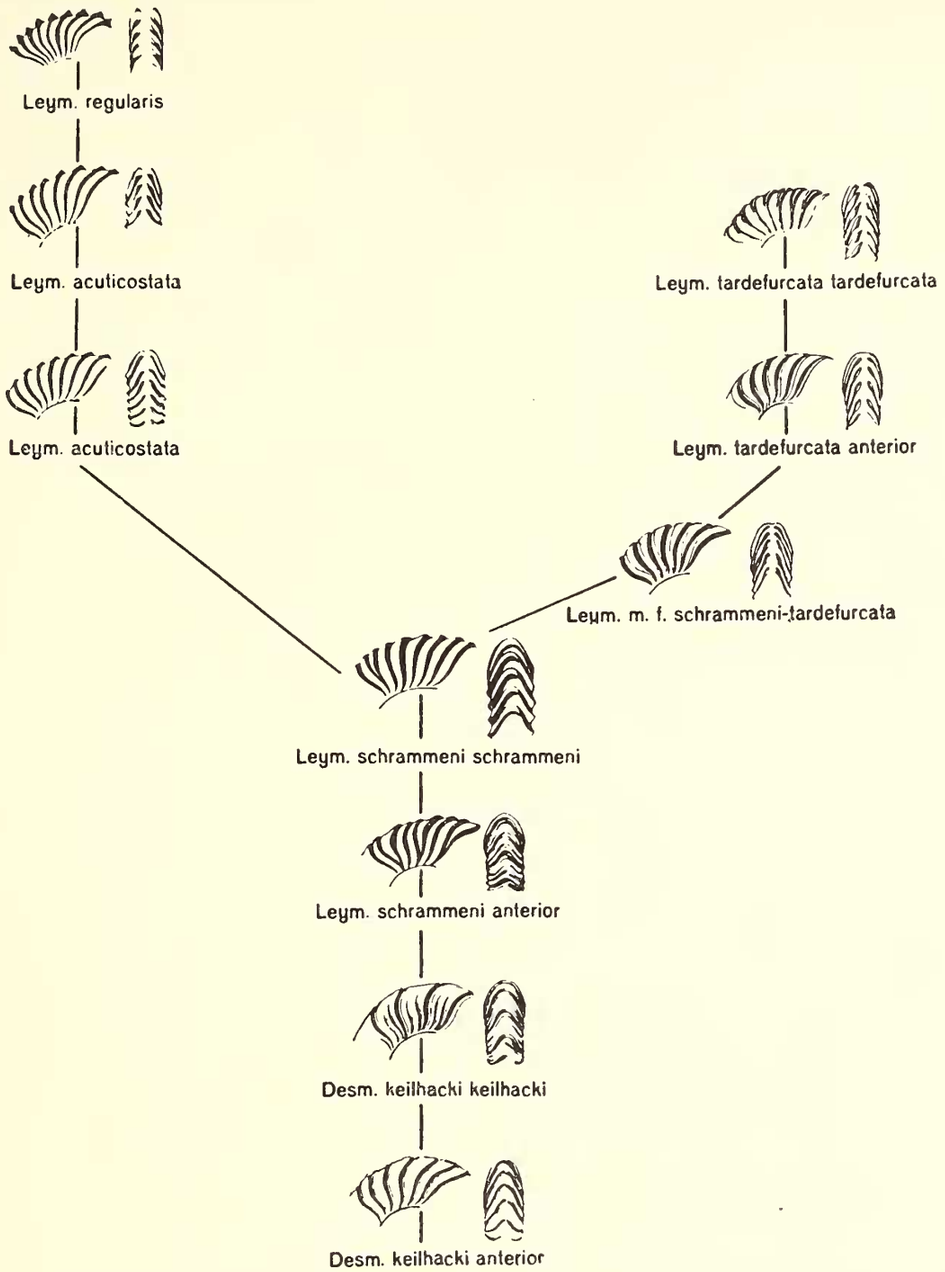
9



9*b*

CASEY, *Leymeriella* from France

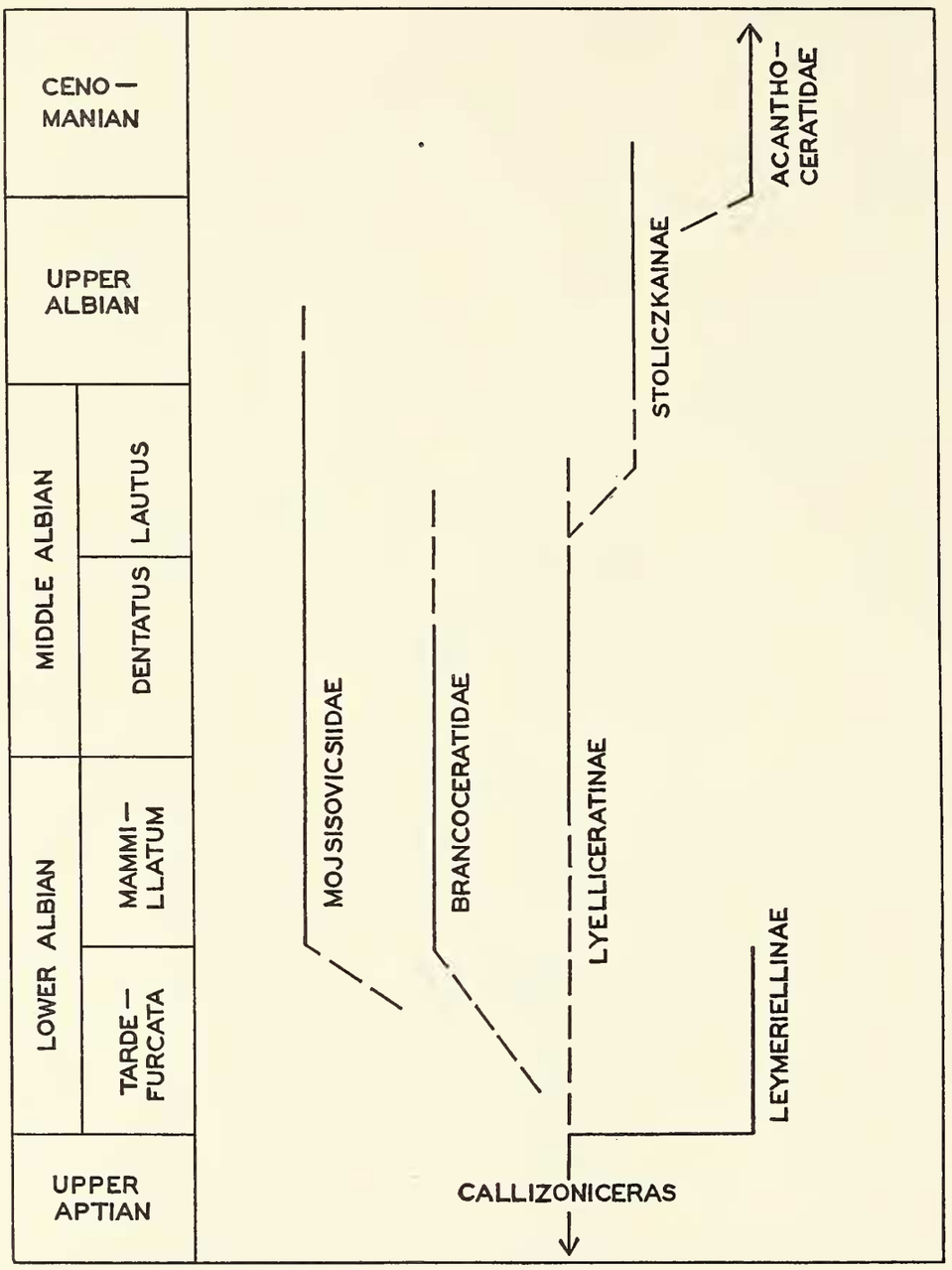
cession of clays that constitute the Upper Aptian and Lower Albian of north Germany provided Brinkmann with a suite of specimens that show a gradual passage upwards from *Callizoniceras* (*Wollemanniceras*) *keilhacki* (Wollemann) of the Jacobi Subzone



TEXT-FIG. 4. Evolution of *Leymeriella* from the Desmoceratid *Callizoniceras*. Copy of Brinkmann 1937, text-fig. 4, p. 6. (For *Desm. keilhacki* read *Callizoniceras keilhacki*; for *Leym. schrammeni* read *Proleymeriella schrammeni*; for *Leym. tardefurcata anterior* read *Leymeriella* (*L.*) *germanica* sp. nov.)

through *Proleymeriella schrammeni* (Jacob) and allies to the typical *Leymeriella* (text-fig. 4). This transformation was achieved by first, the acquisition of strong ribbing, followed by flattening of the ribs and the appearance of a ventral groove, and finally, grooving and tuberculation of the ribs. Discovery of 'gerontic' specimens of *Leymeriella* in the Lower Greensand indicates that the evolution of the genus followed the principle of proterogenesis; if growth proceeded long enough the ammonite returned to a *Proleymeriella* or a *Callizoniceras* condition. Jacob (1908) had already indicated *P. schrammeni*

as the point of origin of *Leymeriella*, but his association of this species with the Aptian Parahoplitidae was ill conceived, as also was Roman's derivation of *Leymeriella* from the Douvilleiceratidae (Roman 1938, p. 360). Brinkmann's results, readily confirmed by a series of duplicate specimens collected in north Germany by Mr. E. V. Wright and



TEXT-FIG. 5. Probable interrelations of early Acanthocerataceae.

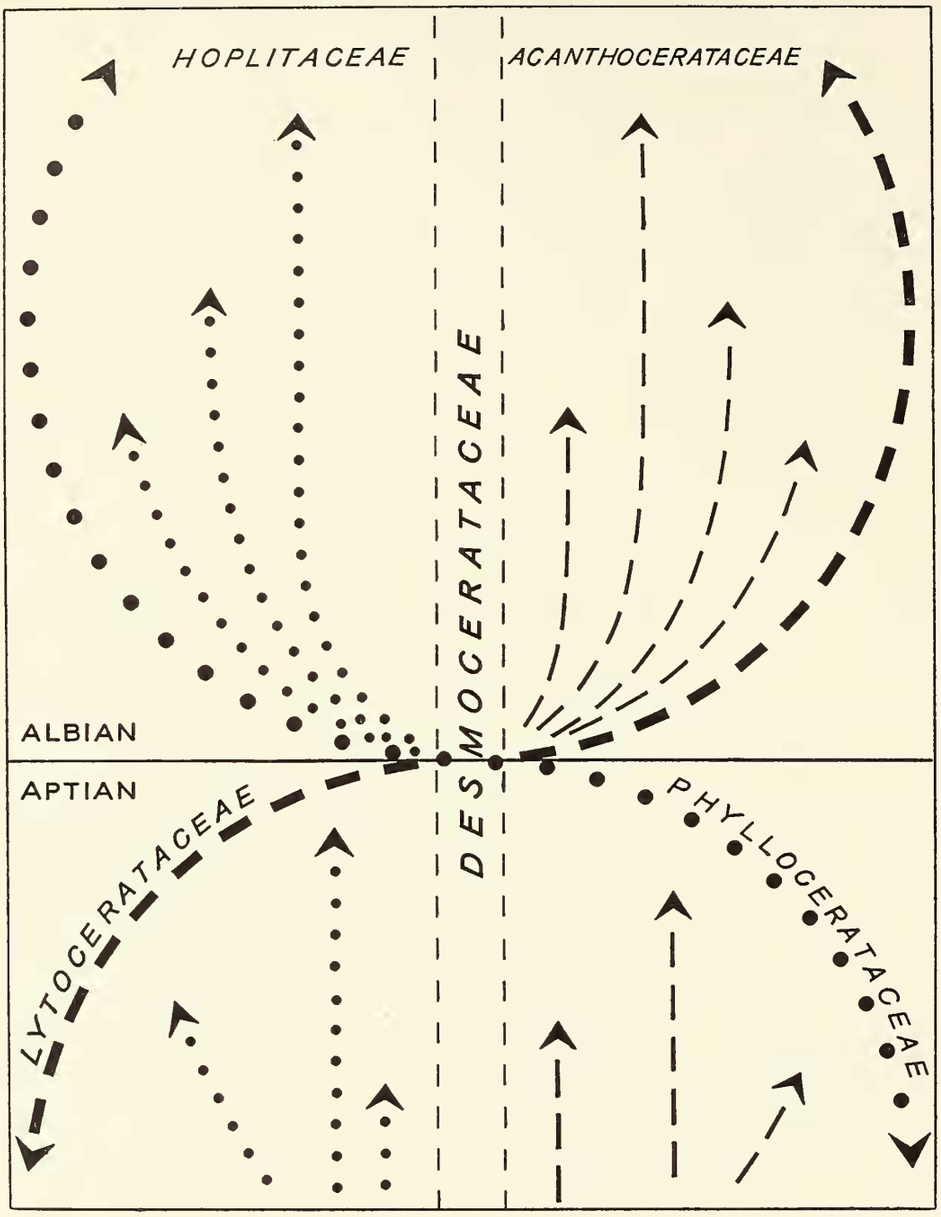
kindly passed to the author for study, take on a new significance in the light of the relationship of *Leymeriella* to *Lyelliceras* and its membership in the Acanthocerataceae. It now seems fair to assume as a working hypothesis that the Lyelliceratidae (including Leymeriellinae), Brancoceratidae, and Mojsisovicsiidae were simultaneous and rapidly differentiating offshoots of a small group of Desmoceratidae centred around *Callizoniceras*. Spath's view as to the common origin of the early Acanthocerataceae and their evolution in the Lower Albian from the Desmoceratidae is thus given strong support, except that emphasis is now placed on *Callizoniceras* rather than *Silesitoides* as the ancestral source. The stratigraphical distribution and probable interrelations of the

family units discussed herein are illustrated diagrammatically in text-fig. 5. Owing to the imperfection of the European record in Lower Albian times, the views here put forward must await confirmation and amplification from other regions.

Evidence of eruptive evolution, expressed in numerous adaptive radiations from a single point of origin, is not confined among Albian ammonites to the Acanthoceratataceae. The trend of research during recent years has been to narrow down the ancestral stock of the Hoplitidae (including Cleoniceratinae) to the Desmoceratid *Uhligella*. Simultaneous with the appearance of *Proleymeriella* at the base of the Tardefurcata Zone is the entry of several branches of the Hoplitinae and Cleoniceratinae showing affiliation to *Uhligella*, notably the genus *Farnhamia* Casey. And it is believed that later Hoplitid genera sprang from these early Tardefurcata Zone prototypes and do not represent successive waves of ornamented Desmoceratids (cf. Casey 1954, p. 107; Wright 1955, p. 571). Apart from genera surviving from the Aptian, it is now possible to visualize the trachyostracous ammonoidea of the Albian as the product of two independent but synchronous radiations from the Desmoceratataceae; one from *Callizoniceras* (Acanthoceratataceae), leading via Lyelliceratidae to the Acanthoceratidae; the other from *Uhligella* (Hoplitaceae), giving rise to the Hoplitidae and thence the Schloenbachiidae and Forbesiceratidae. The Desmoceratataceae were regarded by Spath as a polyphyletic assemblage of derivatives of both Lytoceratataceae and Phylloceratataceae, the two fundamental post-Triassic ammonite stocks (Spath 1923, p. 33), a view shared by the present author, though not by all workers (e.g. Wright 1955). *Callizoniceras* has been claimed as a *Lytoceras* derivative (Salfeld 1924), while *Uhligella* is intimately linked with *Beudanticeras*, which, via forms like *B.* ('*Pseudorbulites*') *convergens* (Jacob) (= *Uhligella convergens* Jacob), shows a passage into the Phylloceratidae. If these affiliations are correctly assessed they carry great implications in the field of ammonite phylogeny, for the picture that now emerges is of an evolutionary stimulus at the commencement of the Albian giving rise to a co-ordinated burst of activity from both the Phylloceratidae and the Lytoceratidae. On the one hand, the Phylloceratid derivatives (Hoplitaceae) retain tight coiling and a suture-line with retracted serial auxiliaries; on the other, the Lytoceratid offshoots (Acanthoceratataceae) betray their origin in their more evolute coiling and simpler suture-line, sometimes (as in adult *Lyelliceras*) with the ancestral bifurcation of the lateral lobes. Text-fig. 6 attempts to illustrate these phylogenetic speculations in diagrammatic form.

It is not proposed on this occasion to discuss fully the various Aptian and Neocomian families that have been at one time or another placed in the Acanthoceratataceae (e.g. Douvilleiceratidae, Pulchelliidae) and now, together with Parahoplitidae and Deshayesitidae, grouped into a heterogeneous 'Hoplitaceae' (Wright 1955, 1957). Unpublished investigation of the Aptian families has shown that they too constitute at least two separate radiations, distinct both from each other and from later radiations in the Albian, though in the case of the Deshayesitidae following a similar course of evolution to that of the Lyelliceratidae. Thus the Deshayesitidae, also springing from *Callizoniceras*, have a *Proleymeriella* phase (*Deshayesites*) and a *Leymeriella* phase (*Dufrenoyia*), and produce multituberculated offshoots (*Cloioceras*, *Somalites*), the latter a homoemorph of *Lyelliceras*. If the pseudoceratitic developments of the Albian and Upper Cretaceous (Engonoceratidae and Placenticeratidae) are indeed the final expression of this Deshayesitid lineage, as has been frequently suggested (just as the Sphenodiscidae

are the pseudoceratitic end-forms of the Acanthocerataceae), it may be necessary to revive for it Hyatt's superfamily name Placenticerataceae (Hyatt 1900, p. 584; published as Placenticeratida).



TEXT-FIG. 6. Hypothetical origin of the Hoplitaceae and Acanthocerataceae in Phylloceratacea and Lytocerataceae respectively, both via the Desmocerataceae.

DISTRIBUTION OF THE LEYMERIELLINAE AND THE ZONAL CLASSIFICATION OF THE LOWER ALBIAN

The Leymeriellinae belong typically to the Northern Hemisphere and are found in deposits of Tardefurcata age that extend from the Urals across Europe westwards to the east coast of Greenland. Penetration to the Equatorial Region, where the Lyelliceratinae, Brancoceratidae, and Mojsisovicsiidae found a congenial habitat, does not seem to have taken place. Records of *Proleymeriella* (*schrammeni* group) from South America (Steinmann 1929, p. 123; Gerth 1935, p. 362) are based on misidentified Brancoceratidae, while the supposed occurrence of *Leymeriella* in Zululand (Haughton 1936, pp. 292–7)

is not supported by illustrations and must be accepted with reservation. Imlay and Reeside's reference to *Leymeriella* in the Queen Charlotte Islands (Imlay and Reeside 1954, p. 230) relate to *Pseudoleymeriella haidaquensis* (Whiteaves).

Occurrences of Leymeriellinae are intimately bound up with the zonal classification of the Lower Albian. Stratigraphers and palaeontologists are not agreed, however, as to the limits of the Lower Albian or as to its zonal subdivisions. In the present paper the Lower Albian substage is given the interpretation placed upon it by Breistroffer (1947) and comprises two zones, *Leymeriella tardefurcata* below and *Douvilleiceras mammillatum* above. The use of *L. tardefurcata* as a zonal index is of long standing and dates at least from von Strombeck (1856).

It is only in north Germany that the vertical distribution of the Leymeriellinae can be followed with any approach to continuity; elsewhere, as in Britain, the record is incomplete, or, as in France, is difficult to decipher owing to condensed deposition. Brinkmann (1937), improving upon the earlier scheme of Stolley (1908), proposed the following classification of the German *Leymeriella* and *Proleymeriella* horizons:

Zones	Subzones
Leymeriella regularis	*Hoplites spp.* *L. hitzeli*
Leymeriella tardefurcata	*L. tardefurcata tardefurcata* *L. tardefurcata anterior*
Leymeriella schrammeni	*L. schrammeni schrammeni* *L. schrammeni anterior*

This classification was emended and simplified by Spath (1942) to conform to the scale of subdivision employed in his comprehensive Albian zonal table. Spath retained a single broad zone of *L. tardefurcata* and recognized three subzones only, in ascending order, *L. schrammeni*, *L. acuticostata*, and *L. regularis*. *L. acuticostata* Brinkmann was chosen as a substitute for Brinkmann's subspecies of *L. tardefurcata* to avoid the use of *L. tardefurcata* both as a zonal and a subzonal fossil.

It must be strongly emphasized that these detailed subdivisions are at present applicable only to north Germany. Outside this area it is only in the topmost part of the Tardefurcata Zone, immediately underlying the Mammillatum Zone, that *Leymeriella* is abundant and widespread. For this part of the succession von Strombeck (1856), Stolley (1908), Spath (1923, 1942), and Brinkmann (1937) all use *L. regularis* as the guide fossil. The term 'Regularis Subzone' for this horizon has become commonplace in British literature. In 1947, however, Breistroffer (1947, pp. 24, 54) proposed to replace *L. regularis* as an index fossil by *L. canteriata* (Defrance) Brongniart sp., the latter being regarded as a senior synonym of *L. pseudoregularis* Seitz. According to this authority, in the Machéroménil district (Ardennes), whence came d'Orbigny's specimens, *L. regularis* is a rare form of the Mammillatum Zone and it is doubtful if it occurs at all in earlier strata. When discussing the faunal sequence of the Lower Albian in general, Breistroffer appears to discredit all records of *L. regularis* from below the Mammillatum Zone and to assume that they refer to *L. canteriata* (= *pseudoregularis*). In 1950 I pointed out (Casey 1950, p. 293) that whatever the zonal origin of d'Orbigny's specimens, there is adequate evidence to show that in England at least both *L. pseudoregularis* and a form indistinguishable from *L. regularis* as figured by d'Orbigny occur side by side *below* the Mammillatum Zone and that no change in zonal nomenclature is required. Further investigation

of this anomalous record of *L. regularis* in the Mammillatum Zone discloses that there is in fact no discrepancy of horizon between the English and French occurrences of *L. regularis*. The apparent discrepancy is due to the failure of French palaeontologists to realize that the Machéroménil fauna, though contained in a single band of phosphatic nodules (Barrois 1878), is condensed and includes not only elements of many different horizons of the Mammillatum Zone but also of the Regularis Subzone of the Tardefurcata Zone. The reasons for this view are as follows:

1. Despite intensive collecting, not a single specimen of *Leymeriella* has been found in the Mammillatum Zone of Kent, where this zone is uncontaminated by fossils derived from the Tardefurcata Zone, though it has yielded every other ammonite genus known in the Mammillatum Zone of Europe, even such exotic genera as *Parengonoceras*, *Tegoceras*, *Uhligella*, and *Oxytropidoceras*.
2. *Leymeriella* is well represented in the Machéroménil assemblage. *Leymeriella regularis*, *L. tardefurcata* (with its var. *intermedia*), *L. consueta* (with its var. *magna*), and *L. rudis* are all present in the collections from this nodule-bed in the Paris Museums. These collections support Barrois's record of *L. regularis* as a common fossil at Machéroménil.
3. Every species and variety of *Leymeriella* found in the 'Mammillatum' nodule-bed of the Ardennes and Meuse Departments of France is found in the Regularis Subzone of southern England.
4. Some of these Machéroménil *Leymeriella* have impressions of other *Leymeriella* in the matrix (see Pl. 8, fig. 3), indicating that they were obtained from 'graveyard' nodules similar to those in the English Regularis Subzone. In no case did I find a Machéroménil *Leymeriella* in the same nodule as a Mammillatum Zone ammonite.

The occurrence of *L. regularis* with Mammillatum Zone ammonites at Machéroménil is thus strictly comparable with its occurrence in Band II at Leighton Buzzard, Beds. (Wright and Wright 1947), or in Bed 7 of Chalvington, Sussex (Casey 1950, p. 276). It

---

EXPLANATION OF PLATE 9

Figs. 1, 1*a*. *Leymeriella* (*Leymeriella*) *tardefurcata* (Leymerie MS.) d'Orbigny, *s.l.* Adult body-chamber showing *Proleymeriella* type of ventral ribbing. Regularis Subzone (Bed 5), Wrecclesham, Surrey. G.S.M. Zm 1309; author's Coll.

Fig. 2. *Leymeriella* (*Leymeriella*) *regularis* (Bruguière) d'Orbigny, condensed Regularis-Mammillatum beds (exact bed unknown), Arnold's Pit, Leighton Buzzard, Beds. B.M. C 40348; G. W. Coles Coll.

Figs. 3, 3*a*. *Leymeriella* (*Leymeriella*) cf. *renascens* Seitz. Locality, horizon, and collector as for Fig. 2. B.M. C. 36627.

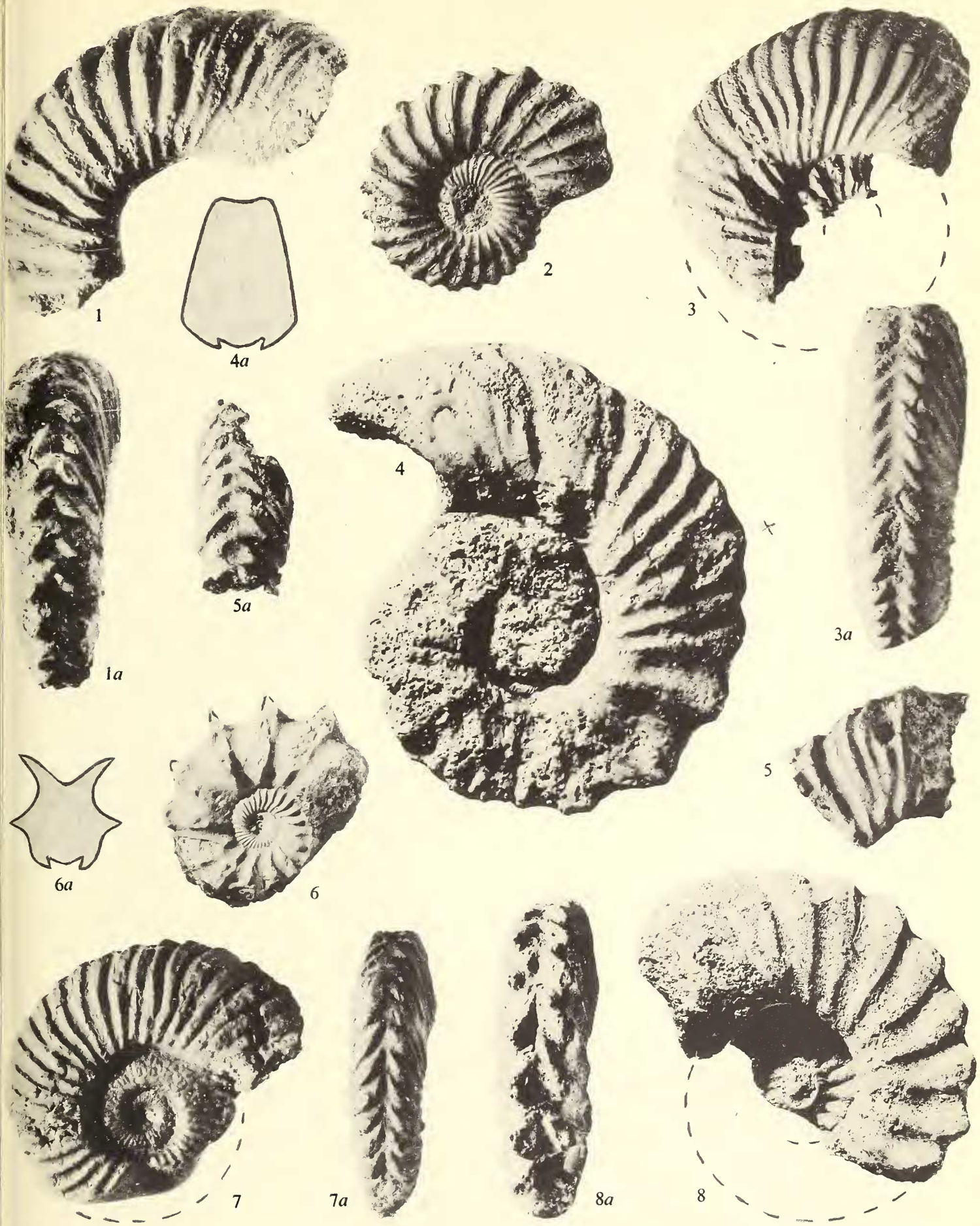
Figs. 4, 4*a*. *Leymeriella* (*Leymeriella*) *consueta* var. *magna* nov. Side view (4), with whorl-section taken at point indicated by *x* (4*a*) of type of variety. Locality and horizon as for Fig. 1. W.W. 20495.

Figs. 5, 5*a*. *Leymeriella* (*Epileymeriella*) cf. *hitzeli* (Jacob). Fragment of adult body-chamber showing *Callizoniceras*-like constrictions and ventral ribbing. Locality and horizon as for Fig. 2. W.W. 15863.

Figs. 6, 6*a*. *Leymeriella* (*Leymeriella*) *diabolus* sp. nov. Side view (6) and restored whorl-section (6*a*) of holotype. Condensed Regularis-Mammillatum beds (Band II), Arnold's Pit, Leighton Buzzard, Beds. W.W. 8084.

Figs. 7, 7*a*. *Leymeriella* (*Leymeriella*) *tardefurcata* var. *densicostata* Spath. Locality and horizon as for Fig. 6. W.W. 16991.

Figs. 8, 8*a*. *Leymeriella* (*Leymeriella*) *consueta* sp. nov. Coarse form leading to var. *magna* nov. Locality, horizon, and collector as for Fig. 1. G.S.M. Zm 1308.



CASEY, *Leymeriella* from Britain

conforms to the familiar pattern of condensed deposition and polyzonal representation so prevalent in the French Albian.

Leymeriella regularis, *L. pseudoregularis*, and *L. tardefurcata* are all associated in the same rock in the derived 'Gault' boulders of Jutland (Skeat and Madsen 1898, pl. 8, pp. 71–74), just as they occur together in England.

Using the threefold subdivision of the Tardefurcata Zone employed by Spath, the following table shows the stratigraphical occurrences of the various genera and species of Leymeriellinae:

	Schrammeni Subzone	*Acuticostata Subzone*	*Regularis Subzone*	*Mammillatum Zone*
Proleymeriella anterior (Brinkmann)	×			
P. schrammeni (Jacob)	×			
P. lemoinei (Jacob)		?		
P. phoenix sp. nov.	×			
Leymeriella (*L.*) *acuticostata* (Brinkmann)		×		
L. (*L.*) *germanica* nom. nov.		×		
L. (*L.*) *tardefurcata* (Leym. MS., d'Orb.)		?	×	
var. *intermedia* Spath			×	
var. *densicostata* Spath			×	
L. (*L.*) *crassa* Spath			×	
L. (*L.*) *romani* Jacob		?	?	
L. (*L.*) *rencurelensis* Jacob		?	×	
L. (*L.*) *revili* Jacob		?	?	
L. (*L.*) *sp. nov.* aff. *revili* Jacob			×	
L. (*L.*) *renascens* Seitz			×	
L. (*L.*) *pseudoregularis* Seitz			×	
L. (*L.*) *heimi* Seitz			?	
L. (*L.*) *fussenegeri* Seitz			?	
L. (*L.*) *andrussovi* Natsky			×	
L. (*L.*) *consueta* sp. nov.			×	
var. *magna* nov.			×	
L. (*L.*) *jacobi* Spath			?	
L. (*L.*) *rudis* sp. nov.			×	
L. (*L.*) *diabolus* sp. nov.			×	
L. (*Epileymeriella*) *hitzeli* Jacob			×	
Pseudoleymeriella haidaquensis (Whiteaves)			?	?

ECOLOGY OF LEYMERIELLINAE

Leymeriella is found in a great variety of neritic deposits, ranging from smooth, soapy clays to coarse sandstones. In Britain and France the principal source of the genus is in the marginal areas of transgression, characterized by shallow-water sediments that carry evidence of inhibited deposition in the presence of glauconite, remanié fossils and rolled phosphatic nodules. At Shenley Hill, Leighton Buzzard, Bedfordshire, where the phosphorite-facies of the Tardefurcata Zone is replaced within a few hundred yards by a brachiopod-rich limestone, the occurrence of *Leymeriella* is exceptional, though it is by no means uncommon in the phosphorites of neighbouring exposures.

There is evidence that the distribution of *Leymeriella* was controlled by ecological factors that acted differentially upon the ammonite faunas. In north Germany, where the development of *Leymeriella* is most complete, the associated ammonite fauna is poor, consisting of species of *Hypacanthoplites* (survivors from the Aptian) and rare *Cleoniceras*; there are no Hoplitinae. On the other hand, during the deposition of the lower

two-thirds of the Tardefurcata Zone Leymeriellinae seem to have been completely excluded from the British area, though free communication with north Germany had been established since Valanginian times. The only known ammonite-bearing deposit of early Tardefurcata age in Europe besides that of north Germany is contained in the Folkestone Beds of the Farnham area of Surrey. Here is preserved a rich fauna dominated by the Hoplitid ammonite *Farnhamia*, together with species of *Hypacanthoplites* and *Anadesmoceras* (Casey 1954, p. 108); there are no Leymeriellinae. Stratigraphical investigations in the Lower Greensand have shown that the supposed association of *Leymeriella* with *Sonneratia* and other Hoplitid genera at the junction of the Tardefurcata and Mammillatum Zones is due to collection from condensed deposits. Wherever the two zones are separated, *Leymeriella* and Hoplitids are never found in association. At Wrecclesham, Surrey, for example, the faunal associates of *Leymeriella* consist of the Cleoniceratids *Anadesmoceras* and *Cleoniceras*, and rare *Hypacanthoplites* and *Pictetia*, and it is only in the overlying nodule-beds of the Mammillatum Zone that Hoplitinae such as *Sonneratia*, *Protohoplites*, *Hemisonneratia*, *and Otohoplites* appear. There is in fact no authenticated record of the occurrence of *Leymeriella* or *Proleymeriella* with a member of the Hoplitinae; for even Skeat and Madsen's '*Hoplites splendens* var. *fittoni*', found with *Leymeriella* in the Jutland Drift is not an *Anahoplites* as supposed by Spath (1943, p. 729) but a species of *Anadesmoceras*. The abrupt exit of *Leymeriella* at the height of its prosperity is no less remarkable than the sudden entry of new, virile Hoplitid stocks in Europe, in the Mammillatum Zone. And since these Hoplitid genera are merely specialized developments from *Farnhamia* of the basal Tardefurcata Zone, it is difficult to avoid the conclusion that the Leymeriellinae and the Hoplitinae were mutually exclusive, the one shunning areas favourable to the other.

SYSTEMATIC ACCOUNT OF BRITISH OCCURRENCES OF *LEYMERIELLA*

In Britain only the Regularis Subzone, the topmost part of the Tardefurcata Zone, yields *Leymeriella*. The principal fossiliferous exposures of this subzone are at Leighton Buzzard, Bedfordshire, and at the village of Wrecclesham, near Farnham, Surrey. The succession at the former locality, described by Lamplugh and Walker (1903), Kitchin and Pringle (1920), and Lamplugh (1922), has been revised in detail by Wright and Wright (1947). The *Leymeriella*-bearing horizons occur at the junction of the Gault and Lower Greensand (Folkestone Beds) and consist of two bands of phosphorite nodules; the lower, Band I, contains Regularis fossils only; the higher, Band II, is a remanié deposit of Regularis and early Mammilatum age. Chamberlain Barn and Arnold's Pits are the chief collecting grounds. The Shenley Limestone of Shenley Hill, Leighton Buzzard, is the approximate lateral equivalent of Band I but yields *Leymeriella* only very rarely. The Wrecclesham occurrence has been described by the author (Casey 1951). Here the Regularis Subzone is preserved at the top of the Folkestone Beds as a thin band of phosphorite nodules (Bed 5) with an underlying zone of incipient phosphatization (Beds 2–4). At the type locality of the Folkestone Beds, at East Cliff, Folkestone, Kent, the Regularis Subzone is represented by about 50 feet of yellowish, coarse sands with bands of glauconitic and calcareous sandstone that yield *Leymeriella* sparingly (Casey 1950). In east Sussex there are poor exposures of a nodule-bed with a remanié fauna of

Regularis-Mammilatum age at the base of the Gault in the neighbourhood of Chalvington and Berwick. Isolated finds of *Leymeriella* have been reported from these exposures (Casey 1950). The slipped section of the Speeton Clay of Speeton, Yorkshire, occasionally affords glimpses of a thin nodular greensand seam (Bed A 4) with rare *Leymeriella* (*Epileymeriella*) cf. *hitzeli* (Jacob). Fossils are very irregularly distributed in these phosphorite beds. I have recorded an instance where several hours' search in the Regularis Subzone of Wrecclesham was rewarded by the discovery of but a single fossiliferous nodule, about three cubic inches in volume, but which contained no less than fourteen small specimens of *Leymeriella* (Casey 1951, p. 98). Such 'graveyard' nodules are familiar to every collector from this horizon. Evidently the beds containing them are the remanié *in situ* of several seams of phosphorite nodules, most of which were unproductive of fossils.

In the following account the symbols G.S.M., B.M., and W.W. are used to discriminate the registration numbers of specimens in the collection of the Geological Survey Museum, the British Museum (Natural History), and the Wright brothers. Measurements of ammonites are given in the following order: diameter in mm., height of the outer whorl, thickness of the same, width of the umbilicus, the last three being in percentages of the diameter. Where two diameters are given, the figure in brackets indicates the size at which the percentages were determined.

For the purposes of zoological nomenclature the term 'variety' as used herein has the status of a subspecies.

Leymeriella (*Leymeriella*) *tardefurcata* (Leymerie MS.) d'Orbigny sp.

Plate 7, fig. 9; Plate 8, figs. 1–3, 8, 8*a*; Plate 9, fig. 1; Plate 10, figs. 10–11

Ammonites tardefurcatus Leymerie, d'Orbigny 1841, p. 248, pl. 71, figs. 4–5.
Ammonites tardefurcatus Leymerie 1842, p. 16, pl. 18, figs. 3*a*, *b*.
Ammonites tardefurcatus Leymerie, Pictet 1847 (*in* Pictet and Roux), p. 76, pl. 7, figs. 4*a*, *b*.
Ammonites canteriatus nudus Quenstedt 1847, p. 152.
non *Hoplites tardefurcatus* Leymerie sp., Wollemann 1904, p. 37, pl. 5, fig. 6.
Hoplites (*Leymeriella*) *tardefurcatus* Leym. sp., Jacob 1908, p. 52, pl. 7, figs. 9–12.
? *Leymeriella tardefurcata* Leym., Sinzow 1913, pl. 4, figs. 37, 37*a*; (*non* figs. 38, 38*a*, 39).
Leymeriella tardefurcata (Leymerie) d'Orbigny sp., Spath 1925, pp. 84–86, pl. 7, fig. 1; pl. 8, fig. 3; text-fig. 17; (*non* pl. 6, fig. 12).
Leymeriella tardefurcata Leym., Roman 1938, p. 361, fig. 36, 341.
Leymeriella tardefurcata (Leym.) d'Orb., Basse 1952, pl. 20, figs. 4, 4*a*.
non *Leymeriella tardefurcata* Leym., Eristavi 1955, p. 135, pl. 6, fig. 11.

Type. Leymerie's example from the Aube, figured by d'Orbigny (1841, pl. 71, figs. 4–5) has been generally quoted as the type of this species (Spath 1925, p. 84; Brinkmann 1937, p. 12; Roman 1938, expl. fig. 36, 341), though there is no record of re-examination of the actual specimen or specimens. D'Orbigny's figures are so often synthetographs that it is doubtful if the citation of one of his illustrations without reference to the original constitutes a valid lectotype designation. My attempts to trace the Leymerie Collection have so far been unsuccessful. The only specimens specifically mentioned by d'Orbigny in his account of the species that I have been able to locate are Raulin's specimens from Varennes (Meuse), now in the École des Mines, Paris. The best of these is here illustrated in Pl. 8, figs. 2, 2*a*, and it may be necessary to select this specimen as neotype if the Leymerie Collection proves to be no longer extant.

Description of typical form. The ammonite is discoidal, compressed, with subrectangular whorl-section and shallow umbilicus. The whorl reaches its greatest thickness just above the umbilicus and from here the flattened sides narrow slightly to a subtabulate venter that bears a rounded median concavity. For the greater part of life the umbilicus measures about one-third the diameter, but dilates at maturity; the umbilical wall, at first low, fairly steep, and rounded, later becomes flat and oblique. Costation is close, about 35 ribs at 30 mm. diameter, 40 at 50 mm. diameter. The ribs commence at the umbilical suture and are inclined forwards on the flank. They are thin and sharp on the lower part of the flank, but from a point just below mid-flank they expand into narrow, flattened, sulcate wedges. The course of the ribs across the flank varies from almost straight, through slightly curved to gently sigmoidal. Ventrally the ribs terminate in slight clavi that are directed slant-wise forwards across the venter, but fail to connect, leaving a smooth siphonal band. At very large diameters there may be a return to a *Proleymeriella* type of ornament, with shallow constrictions, no tubercles, and the ribs united in chevrons across the venter. A broad, bifid external saddle and small, nearly symmetrical, trifid first lateral lobe characterize the suture-line.

Measurements

W.W. 13603	*c.* 60 (50),	·40,	·33,	·38	Leighton Buzzard. One-third whorl body-chamber.
„	(30),	·40,	?,	·33	
Jacob, pl. 8, fig. 12	35,	·40,	·29,	·29	Près de Rencurel (Isère).
Raulin Coll. (École des Mines)	30,	·40,	·30,	·33	Varennes (Meuse). Septate.
G.S.M. 31606	21,	·40,	·30,	·30	Leighton Buzzard. Septate.

Remarks. Although d'Orbigny credited the combination *Ammonites tardefurcatus* to Leymerie, his own description and illustration of the species in 1841 first gave validity to the name and established d'Orbigny as its author for the purposes of zoological nomenclature. Nevertheless, most authors who have discussed this nominal species attribute it to Leymerie, whose account appeared in 1842 (Leymerie 1842, p. 16, pl. 18, figs. 3*a–b*).

The many records of *L. tardefurcata* from England, France, Switzerland, Germany, and Transcaspia, not to mention reports of the species from the Carpathians, the Urals, and Greenland, would lead one to suppose that this ammonite is well documented and fully described. On the contrary, despite its frequent citation in the literature and its use in stratigraphy, it cannot be considered adequately known. It has been rarely figured photographically, and then only by immature specimens. Jacob's Isère example of 35 mm. (Jacob 1908, pl. 7, figs. 12*a–c*) is not fully grown as he supposed, for specimens of twice that size are found in the Lower Greensand. In the absence of adult topotype material for comparison, however, the identification of the larger Lower Greensand specimens is perhaps not above criticism. A Leighton Buzzard example of 60 mm. diameter (Pl. 10, fig. 11) shows a sudden change to a much coarser style of ribbing on the body-chamber, and in an even larger specimen from Wrecclesham (Pl. 9, figs. 1, 1*a*) this coarse stage is followed again by closer ribbing, now uniting in chevrons on the venter in the manner of *Proleymeriella*. If the characters of these two specimens typify those of the normal adult *L. tardefurcata* the 'varieties' *intermedia* and *densicostata*, discussed below, are probably too distinct to be united with this species.

Apart from the named varieties just mentioned, *L. tardefurcata* s.s. itself shows a certain amount of mutability. This occurs principally in two features, the flexuosity of the ribbing and the diameter at which the umbilical wall takes on a gentle gradient. There are also passage forms to the var. *intermedia* and var. *densicostata*, both distinguished by more open umbilici and, in the one case, more distant, and in the other, closer ribbing on the inner whorls.

Strictly interpreted, *L. tardefurcata* is a fossil of the Regularis Subzone and records of the species from earlier strata require confirmation. The use of *L. tardefurcata* as a zonal or subzonal index fossil for beds below the level of *L. regularis* in Germany (Stolley 1908; Brinkmann 1937) and France (Breistroffer 1947) is open to challenge. Collections of *Leymeriella* from the middle of the Tardefurcata Zone of north Germany examined by me in the Paris museums and in the possession of the Wright brothers do not contain a single specimen of the true *L. tardefurcata*, although there are a number of *tardefurcata*-like forms, including *L. germanica* nom. nov. (= *L. tardefurcata anterior* Brinkmann (1937, p. 9, fig. 9). The subspecific name *anterior* was already employed by Brinkmann in the combination *Leymeriella schrammeni anterior* and cannot be used again in the same genus.) Owing to the prevalence of condensed deposition in the *Leymeriella*-bearing beds of France, records of the present species from that country give inconclusive evidence of horizon.

Leymeriella (*Leymeriella*) *tardefurcata* var. *densicostata* Spath

Plate 9, figs. 7, 7*a*; Plate 10, figs. 9, 9*a*, 12

Hoplites (*Leymeriella*) *tardefurcatus* Leym. sp., variété à côtes serrées, Jacob 1908, pl. 7, figs. 13*a*, *b*.

Leymeriella tardefurcata (Leymerie) d'Orbigny sp. var. *densicostata* Spath 1925, p. 85, pl. 7, fig. 2.

Leymeriella tardefurcata Leym. in d'Orb. sp. var. *densicostata* Spath, Breistroffer 1931, p. 194.

Leymeriella tardefurcata Leym. sp. var. *densicostata* Spath, Breistroffer 1947, p. 23.

Type. The example figured by Spath (1925, pl. 7, fig. 2) from the condensed Tardefurcata-Mammillatum Zones of Chamberlain Barn Pit, Leighton Buzzard, Beds. (L. F. Spath Coll. no. 977).

Description. This variety is distinguished by the relatively rapid widening of its umbilicus and by its densely ribbed inner whorls, possessing 50–55 ribs at 30 mm. diameter as compared with an average of 35 in the typical form.

Measurements

W.W. 16991	47, ·40, ·28, ·40	Leighton Buzzard. Half-whorl body-chamber.
W.W. 19703	27, ·42, ·30, ·30	Leighton Buzzard (Band II).

Remarks. Specimens of this variety hitherto figured and described are immature. It is now possible to see from material more representative of the different stages of growth that the dense ribbing which makes this variety so easily separable at 30 mm. diameter does not persist into the adult, which at 40–50 mm. diameter has costation precisely the same as that of the typical *L. tardefurcata*. A Wrecclesham example (G.S.M. Zm 1286), previously recorded (Casey 1951, p. 97) as *L.* aff. *tardefurcata*, has dimensions 53, ·39,

·30, ·34, and is intermediate between this var. *densicostata* and *L. tardefurcata* s.s. Specialization in dense ribbing is carried to a more advanced stage in *L. revili* Jacob (1908, pl. 7, figs. 16*a*, *b*).

Leymeriella (*Leymeriella*) *tardefurcata* var. *intermedia* Spath

Plate 10, figs. 2, 6, 8, 8*a*

? *Ammonites canteriatus* Brongniart, Quenstedt 1849, pl. 10, figs. 13*a*, *b*.
? *Leymeriella tardefurcata* Leym., Sinzow 1913, pl. 4, fig. 39 only.
Leymeriella tardefurcata (Leymerie) d'Orbigny sp. var. *intermedia* Spath 1925, p. 85 (pars) pl. 6, fig. 12.
Leymeriella tardefurcata intermedia Spath, Wright and Wright 1947, p. 166 (pars).
Leymeriella intermedia Spath, Casey 1951, p. 97 (pars).

Type. The example figured by Spath (1925, pl. 6, fig. 12) from the condensed Tardefurcata-Mammillatum Zones of Billington Crossing, Leighton Buzzard, Beds. (G. W. Lamplugh Coll.).

Description. This variety is characterized by the relatively rapid widening of the umbilicus and by having inner whorls that are slightly more coarsely ribbed, bear more distinct peripheral clavi, and give a hint of tuberculation just above the umbilicus.

EXPLANATION OF PLATE 10

Fig. 1. *Leymeriella* (*Leymeriella*) *pseudoregularis* Seitz. Adult example. Regularis Subzone (Bed 5), Wrecclesham, Surrey. G.S.M. Zm 1289; author's Coll.

Fig. 2. *Leymeriella* (*Leymeriella*) *tardefurcata* var. *intermedia* Spath. Dwarf form. Regularis Subzone (Band I), Arnold's Pit, Leighton Buzzard, Beds. W.W. 18038.

Figs. 3, 3*a*. *Leymeriella* (*Leymeriella*) *consueta* var. *magna* nov. Adolescent body-chamber. Locality, horizon, and collector as for Fig. 1. G.S.M. Zm 1295.

Fig. 4. *Leymeriella* (*Leymeriella*) *renascens* Seitz. Condensed Regularis-Mammillatum beds (exact bed unknown), Arnold's Pit, Leighton Buzzard, Beds. W.W. 16106.

Figs. 5, 5*a–b*. *Leymeriella* (*Leymeriella*) *consueta* sp. nov. Side view (5), ventral view (5*b*), and whorl-section (5*c*) of nucleus. Regularis Subzone (Band I), Arnold's Pit, Leighton Buzzard, Beds. W.W. 9741.

Fig. 6. *Leymeriella* (*Leymeriella*) *tardefurcata* var. *intermedia* Spath. Adult example. Locality and horizon as for Fig. 5. W.W. 17949.

Fig. 7. *Leymeriella* (*Leymeriella*) *regularis* (Bruguière) d'Orbigny sp. Body-chamber fragment. Locality, horizon, and collector as for Fig. 1. G.S.M. Zm 1306.

Figs. 8, 8*a*. *Leymeriella* (*Leymeriella*) *tardefurcata* var. *intermedia* Spath. Coarsely ribbed form leading to *L.* (*L.*) *regularis*. Locality, horizon, and collector as for Fig. 1. G.S.M. Zm 1288.

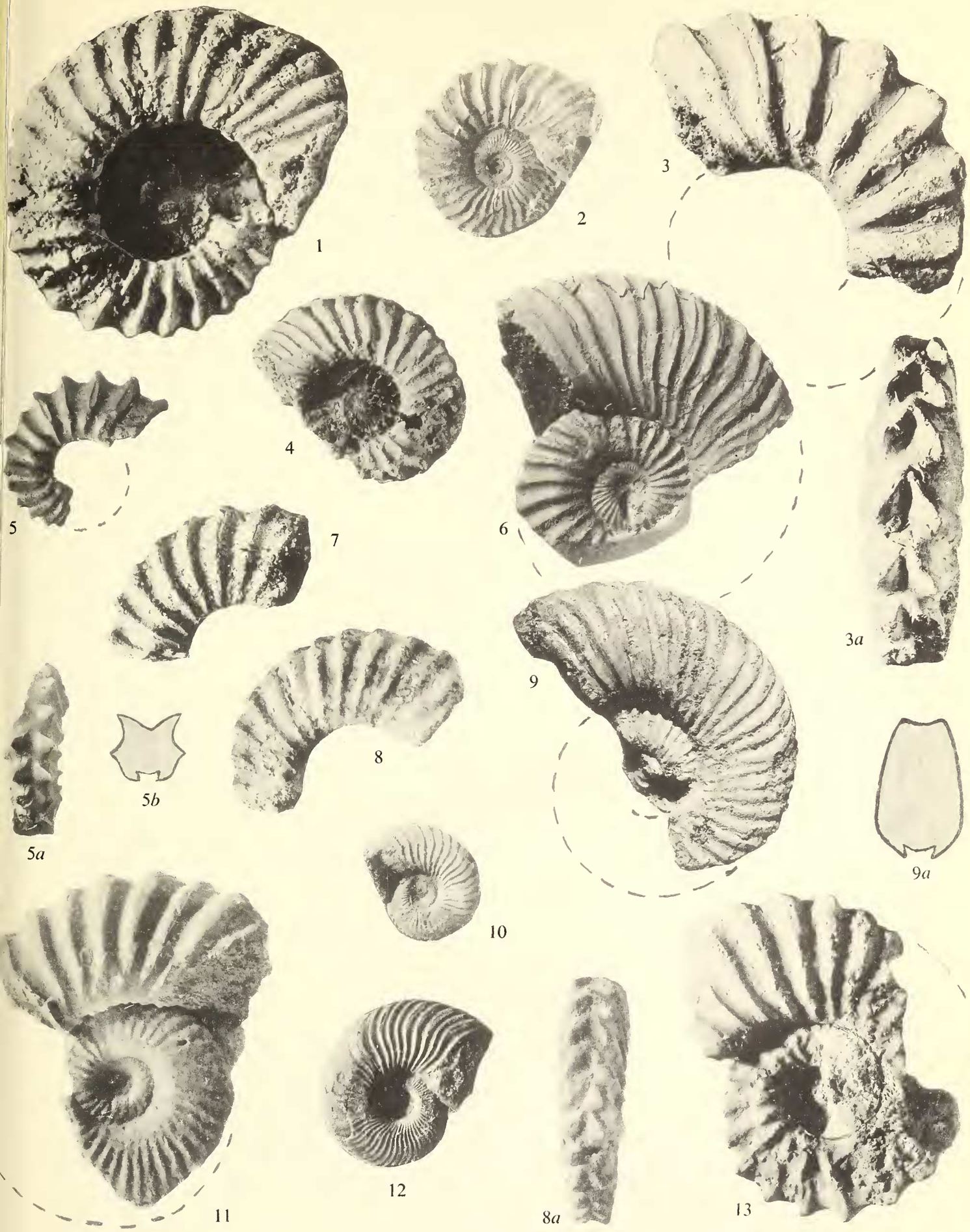
Figs. 9, 9*a*. *Leymeriella* (*Leymeriella*) *tardefurcata* var. *densicostata* Spath. Side view (9) and whorl-section (9*a*) of example with coarsely ribbed inner whorls, transitional from *L.* (*L.*) *tardefurcata* s.s. Regularis Subzone (Bed 4), Wrecclesham, Surrey. G.S.M. Zm 1286; author's Coll.

Fig. 10. *Leymeriella* (*Leymeriella*) *tardefurcata* (Leymerie MS.) d'Orbigny sp. Immature example. Locality and horizon as for Fig. 4. G.S.M. 31606.

Fig. 11. *Leymeriella* (*Leymeriella*) *tardefurcata* (Leymerie MS.) d'Orbigny sp. *s.l.* Large example showing coarsely ribbed body-chamber. Locality and horizon as for Fig. 4. W.W. 13603.

Fig. 12. *Leymeriella* (*Leymeriella*) *tardefurcata* var. *densicostata* Spath. Immature example. Condensed Regularis-Mammillatum Beds (Band II), Arnold's Pit, Leighton Buzzard, Beds. W.W. 19703.

Fig. 13. *Leymeriella* (*Leymeriella*) *consueta* sp. nov. Holotype. Locality, horizon, and collector as for Fig. 1. G.S.M. Zm 1307.



CASEY, *Leymeriella* from Britain

Measurements

W.W. 17949	*c.* 55 (46), ·38, ·30, ·39	Leighton Buzzard (Band I). Half-whorl body-chamber.
D'Orbigny Coll.	47, ·38, ·29, ·40	Machéroménil. Half-whorl body-chamber.
W.W. 16038	27, ·38, ·27, ·39	Leighton Buzzard. Half-whorl body-chamber.

Remarks. This variety links *L. tardefurcata* with *L. regularis*, though morphologically it is closer to the former of the two. In the case of immature or fragmentary material identification of this variety should not lightly be attempted, for it is not distinguished from *L. consueta* until 20 mm. diameter, while the coarsely ribbed stage which is its chief point of difference from *L. tardefurcata* s.s. is transitory, and although of variable duration is always confined to the young. Normally, by 30 mm. diameter the costation is no different from that of the typical *L. tardefurcata*, though in transitions to *L. regularis* it may remain distinct until 45 mm. diameter. On the other hand, variation in the opposite direction leads to a form like that from Machéroménil illustrated in Pl. 8, fig. 1. This is separable from *L. tardefurcata* s.s. only by the wider umbilicus and the slightly emphasized ventral clavi of the young.

The small example listed in the table of measurements and illustrated in Pl. 10, fig. 2 is a dwarf. The open umbilicus and closing up of the ribs towards the end indicate that it is fully grown at 27 mm. diameter.

Leymeriella fussenegeri Seitz, from Vorarlberg (Rhaetic Alps), seems to be one of these transitions from *L. tardefurcata* var. *intermedia* to *L. regularis*, differing from the typical form of *intermedia* only in its more definite suggestion of bituberculation on the inner whorls. It is doubtful if it merits a separate name.

Leymeriella rencurelensis Jacob is allied to this variety, but has uniformly coarse ribbing and stouter whorls. Jacob's fragment of '*Hoplites* (*Parahoplites*) sp.' from Isère (Jacob 1908, pl. 7, figs. 5*a–b*), renamed *Leymeriella jacobi* by Spath (1925, p. 75), seems to be distinguishable from the present form at 45 mm. diameter only by a small increase in the thickness of the whorl.

Distribution. (Typical form and var. *intermedia*) ubiquitous in the Regularis Subzone of south-east England. (Var. *densicostata*) Band II, Arnold's Pit, Billington Crossing, Leighton Buzzard, Bedfordshire, and Bed 4, Wrecclesham, Surrey.

Leymeriella (*Leymeriella*) *regularis* (Bruguière) d'Orbigny sp.

Plate 8, figs. 5, 5*a*, *b*, 9, 9*a*; Plate 9, fig. 2; Plate 10, fig. 7

? *Ammonis cornu* Langius 1708, p. 95, pl. 24, fig. 2.
? *Ammonites regularis* Bruguière 1789, p. 42, no. 19.
? *Ammonites canteriatus* (Defrance), Brongniart (*in* Cuvier and Brongniart) 1882, pl. 6, fig. 7.
Ammonites regularis Bruguière, d'Orbigny 1841, p. 245, pl. 71, figs. 1, 2 (not fig. 3).
Ammonites canteriatus nodosus Quenstedt 1847, p. 152.
Hoplites regularis Brug., Skeat and Madson 1898, p. 198 (pars), pl. 8, figs. 6, 8 (only).
non *Hoplites* (*Leymeriella*) *regularis* Brug. sp., Jacob 1908, pl. 17, figs. 23–24.
Leymeriella regularis (Bruguière) d'Orbigny sp., Spath 1925, p. 86, pl. 6, figs. 13*a*, *b*; pl. 8, fig. 4; text-fig. 18 (*non* pl. 7, fig. 3).
non *Leymeriella regularis* (Brug.) d'Orb., Seitz 1930, p. 21, pl. 4, figs. 2*a*, *b*; text-fig. 3*a*.
Leymeriella aff. *regularis* Bruguière, d'Orbigny sp., Casey 1950, p. 292, pl. 14, figs. 11*a*, *b*.

Neotype (here selected). A specimen in the Raulin Collection in the École des Mines, Paris (Pl. 8, figs. 5, 5*a–b*) from the condensed Tardefurcata-Mammillatum Zones of Sauces, near Novion (Ardennes), apparently used for d'Orbigny's pl. 71, figs. 1–2.

Description. To a diameter of 12–15 mm. this species resembles *L. tardefurcata*. Thereafter the ribbing becomes increasingly distantly spaced, and the appearance of umbilical flares and ventral clavi cause the whorl-section to change from subrectangular to hexagonal. When the ornament is fully developed, at 25–30 mm. diameter, the whorls bulge at the umbilical flares, are slightly concave at the sides, and have the venter excavated in the form of a V. The ribs commence just above the umbilical suture and lean forwards as they cross the gentle umbilical slope to merge into the umbilical flare; here they are thin and sharp. On leaving the umbilical flare they strike across the flank in a line that is almost straight or gently concave forwards; here they are flat, ribbon-like, broaden towards the venter and bear a shallow median depression. At the ventro-lateral margins they are elevated into prominent triangular clavi that lean outwards from the flank and are prolonged faintly obliquely forwards on the venter, each pair of clavi thus producing a faint chevron with the apex cut off by the bottom of the ventral sulcus. At 35 mm. diameter the ribs number 20–25. The umbilicus is at first about one-third of the diameter, but widens a little during growth. Decline in strength of the sculpture takes place at varying diameters after 25 mm. The umbilical flares lose height and move closer to the margin of the umbilicus, the umbilical slope becomes steeper, the ventral clavi less projecting, and the costation more closely spaced.

Measurements

B.M. C 40348	*c.* 40 (36), ·40, ·33, ·36	Leighton Buzzard.	Half-whorl body-chamber
Neotype	35, ·40, ?, ·35	Sauces (Ardennes).	,, ,,
W.W. 18812	30, ·40, ·33, ·34	Leighton Buzzard.	,, ,,
G.S.M. 31607	27, ·39, ·33, ·33	,, ,,	,, ,,
B.M. L.F.S. 986	21, ·40, ·32, ·32	,, ,,	,, ,,

Remarks. Leymeriella regularis is involved in difficulties all too familiar to the palaeontologist dealing with old-established specific names. Its use in stratigraphy as an index fossil is threatened both by doubts as to the identity of the species which should rightfully bear the name and by conflicting opinions as to the horizon of the species which customarily passes for *L. regularis*.

Bruguière did not himself illustrate the species when proposing the name *Ammonites regularis*, but referred to a specimen figured in an early-eighteenth-century work (Langius 1708, pl. 24, fig. 3). This specimen is no longer extant and the illustration is quite inadequate for recognition of the species by present-day standards. The modern interpretation of *A. regularis* dates from its illustration by d'Orbigny (1841, pl. 71, figs. 1–3) and it is d'Orbigny's original, from the Albian of the Ardennes, which for over a century has assumed the role of type specimen. Although the great majority of workers have been content to accept d'Orbigny's authority concerning the identity of *A. regularis*, Quenstedt was a dissentient. He supposed Langius's original to be a Liassic *Schlotheimia* and regarded d'Orbigny's specimen as a variety of *A. canteriatus* Defrance, styling it

A. canteriatus nodosus. Owing to the prior use of the name *Ammonites nodosus* by de Roissy (1805), Schlotheim (1813), and J. Sowerby (1815), we are not obliged to revive Quenstedt's name for this species.

I am of the opinion that in view of its use in stratigraphy and long standing in the literature, the name *A. regularis* should be retained with the meaning given it by the majority of workers. Application will therefore be made to the International Commission on Zoological Nomenclature for the recognition of a neotype selection for *A. regularis* that will realize this objective. The original (or one of the originals) of d'Orbigny's pl. 71, figs. 1–2 is the ideal choice for neotype.

D'Orbigny (1841, p. 248) stated that his figured specimen had been collected by J. Raulin from Sauces, in the Machéroménil neighbourhood of the Department of Ardennes, that it retained the test, and that it was reproduced natural size. The École des Mines, Paris, possesses a specimen of *L. regularis* in the Raulin Collection from that locality. It has the test preserved and was almost certainly used in d'Orbigny's illustration. The specimen is partly enclosed in a phosphorite nodule and ends at a natural break at about 35 mm. diameter. This break runs obliquely forwards and downwards and corresponds to the crack illustrated in d'Orbigny's drawing at 42 mm. diameter. In my opinion d'Orbigny's illustration is a synthetograph, composed of a slightly enlarged reproduction of Raulin's specimen with the last half-whorl added from another specimen or from imagination. I have seen no examples of *L. regularis* as large as d'Orbigny's holograph, and it is possible that this last half-whorl was restored from a specimen of *L. consueta*, specimens of which are labelled *A. regularis* in the d'Orbigny Collection. I believe that the suture-line (d'Orbigny 1841, pl. 71, fig. 3) attributed to *A. regularis* was drawn from the holotype of *L. rudis* sp. nov., another of d'Orbigny's Machéroménil '*A. regularis*'. It is proposed to designate the specimen in the Raulin Collection (Pl. 8, figs. 5, 5*a*, *b*) neotype of *A. regularis* Bruguière.

A form of *Leymeriella* differing from *L. regularis* in its greatly increased whorl-thickness was separated by Spath (1925, p. 87) under the name *L. regularis* var. *crassa*. To this variety were referred Jacob's *forme épaisse* of *L. regularis* and a single specimen from Leighton Buzzard. The latter is an execrable fragment, hardly more than 22 mm. in diameter, and was illustrated by Spath only in a sectional outline, enlarged and greatly restored (Spath 1925, pl. 7, fig. 3). Up to 20 mm. diameter the specimen exhibits characters normal to a compressed *Leymeriella* of the *regularis-consueta* type; on the final portion of the ammonite the whorl suddenly expands and at the same time the sides develop crippled ribs. It is an obvious malformation. Despite the fact that this specimen is labelled 'holotype' in the British Museum collections, we are not bound to accept it as such, since no type selection was made either in the original or in subsequent publications. Jacob's *L. regularis, forme épaisse*, from Goudinière (Haute-Savoie) (Jacob 1908, pl. 7, figs. 24*a*, *b*), one of the syntypes of this 'variety', is here designated lectotype of *L. crassa* Spath. In according this taxon specific rank I follow Breistroffer (1947, p. 70), for *L. crassa* is not only more inflated than *L. regularis*, but also more strongly tuberculate, its ribs more deeply sulcate. The species has not yet been found in England.

Distribution. Regularis Subzone. Folkestone Beds (Bottom Stone Band), East Cliff and Mill Point, Folkestone; Beds 4 and 5, Wrecclesham, Surrey; Bed 7, Chalvington, Sussex; Bands I and II, Arnold's and Chamberlain Barn Pits, Leighton Buzzard, Bedfordshire.